



Do growth rate and survival differ between undisturbed and disturbed environments for *Sceloporus spinosus* Wiegmann, 1828 (Squamata: Phrynosomatidae) from Oaxaca, Mexico?

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Abstract.—Demography is intimately related to the evolution of the life history of a species, since it describes the patterns of variation in the growth, maturation, reproduction, and survival of an organism through populations, species, and environments. In this study the growth, survivorship, and population structure were evaluated for an oviparous lizard, *Sceloporus spinosus* from two sites, a relatively undisturbed area (UA) and a disturbed area (DA; zone of land-use change) within the Natural Protected Area Yagul of southern Oaxaca, Mexico. The results showed different relative densities between seasons (higher during the wet season than the dry season), but not between populations. Males and females from the UA and DA showed similar growth rate patterns, and both sexes reached sexual maturity at a similar body size. The highest survival rates and recapture probabilities were found in the UA; however, males from both populations showed higher survival rates than females. Overall, this study suggests that land-use changes do not seem to cause wide variation in the analyzed demographic characteristics of this species. This work describes and quantifies demographic effects on some life history characteristics of a species endemic to Mexico. We argue for the need to analyze and compare many capture-recapture data for a species between locations in order to obtain a better assessment of the variation in the life history characteristics analyzed.

Keywords. Age class, Cormack-Jolly-Seber model, demography, density, natural protected area, toe-clipping method

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Introduction

The variation in life history characteristics of lizards is considered to be an outcome of phenotypic plasticity driven by changing environmental conditions (Stearns 1992; Adolph and Porter 1996). Studies investigating demographic parameters (e.g., density, sex ratio, natality, growth rate, age classes) and life history (e.g., SVL at sexual maturity, survival, reproduction, fecundity) in lizards have shown that different life strategies (e.g., growth rate, survival) in these vertebrates have evolved due to environmental changes caused by habitat loss and by changes in land use (Dunham 1982; Stearns 1992). This implies that the populations of any species may evolve different life history strategies according to the

characteristics of the environments that they inhabit (e.g., pristine or fragmented). Therefore, the conservation priority of populations of a widely distributed species, is to assess the tolerance of their life history characteristics to certain environmental factors (precipitation, humidity, radiation, pollution, deforestation, and others) that occur throughout the distribution of the species; therefore, this is a feasible method to test for changes in their fitness (Walkup et al. 2017). Evolution within and across species that inhabit fluctuating environments has resulted in changes of their life history strategies, such as size and age at sexual maturity, fecundity (clutch size), growth rate, and survival (Stearns 1992); and these changes have been found within different populations of a single species that is widely distributed (Dunham 1982; Cruz

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et al. 2014; Pérez-Mendoza et al. 2014; Cruz-Elizalde and Ramírez-Bautista 2016). These variations in life history characteristics have been documented in several species that inhabit environments with different degrees of disturbance (Cruz et al. 2014; Cruz-Elizalde and Ramírez-Bautista 2016; Walkup et al. 2017). However, strong fragmentation of habitats by land use change, pollution, and global warming have adverse effects on these strategies, that consequently lead to population decline at the local level (Sinervo et al. 2010).

Due to concerns regarding the effects of environmental disturbances, some researchers have generated conservation models for various biological groups (e.g., birds, Escalante et al. 1998; mammals, Ceballos and Oliva 2005) that include significant amounts of information on the natural history of individual species. For example, Sinervo et al. (2010) described patterns of species decline and extinction in a diverse assemblage of lizard species of genus *Sceloporus* under thermoregulatory stress induced by global warming. Chávez (2011) and Calderón-Mandujano (2011) noted that land use change is another factor that has resulted in high levels of population decimation and extinction among lizards and amphibians. However, each species responds in different ways according to the pressures of their local environment (Tews et al. 2004; Suazo-Ortuño et al. 2007). This pattern has been documented in several wide-ranging species that occur in relatively pristine habitats as well as sites that are subject to varying degrees of disturbance (e.g., *Sceloporus grammicus*, Pérez-Mendoza et al. 2014; *S. minor*, García-Rosales et al. 2017; and *S. variabilis*, Cruz-Elizalde and Ramírez-Bautista 2016). Therefore, considering these factors, herein, the effects of a pristine and a disturbed habitat on some life history characteristics were evaluated in two populations of *Sceloporus spinosus* (Eastern Spiny Lizard) in southeastern Mexico.

Sceloporus spinosus is a species endemic to Mexico, and adults are of medium body size for the genus (120 mm snout-vent length, SVL; Ramírez-Bautista et al. 2014). The scales of the body are strongly keeled and mucronate. This species feeds on insects and other invertebrates, and it is oviparous with a clutch size of eight to 31 eggs and a mean of 18.5 (Valdéz-González and Ramírez-Bautista 2002). This lizard is found from Durango to Oaxaca, and inhabits arboreal and saxicolous landscapes (Torres-Barragán 2015) in both temperate and semiarid regions, at an elevation range from 1,900 to 2,700 m (Canseco-Márquez and Gutiérrez-Mayén 2010). In Yagul Natural Protected Area (NPA), this species is distributed in a mountain range with elevations from 1,600 to 2,000 m. So far, there is limited information regarding demographic aspects of this species in pristine and disturbed areas such as Yagul NPA. In this framework, the goal of this study was to compare and assess key demographic characteristics, such as density, growth, survival, and population structure of *S. spinosus* in two

contrasting environments, in Oaxaca, Mexico. Therefore, considering that land use change promotes variation in demographic characteristics and life histories in various vertebrate groups (Adolph and Porter 1996; Flatt and Heyland 2011), these demographic characteristics were expected to differ as a function of the environments where each population of *Sceloporus spinosus* occurred.

Materials and Methods

Study Area

This study was carried out at two sites in Yagul Natural Protected Area in the municipality of Tlacolula de Matamoros, Oaxaca, Mexico (Fig. 1). The municipality encompasses 1,076 ha, ranging in elevation from 600 to 2,500 m. The vegetation at the site is represented by tropical dry forest; however, much of it has been replaced by crops and grazing areas. The climate is semi-warm, with temperatures ranging from 16 °C to 26 °C, and mean annual precipitation from 400 to 800 mm (INEGI 2005).

Two sites of 1 ha each were chosen for this study. The first site was considered the undisturbed area (UA; 16.957922 N, -96.429953 W; 1,800 m), with a vegetation cover of 83% and an arboreal density of 697 individual trees/ha. This cover includes 80% tropical dry forest, 10% flood zone, 3% reedbed (*Arundo donax*), and 2% surface without vegetation (Torres-Barragán 2015). The second site was a disturbed area (DA; 16.959617 N, -96.450633 W; 1,652 m; Fig. 1). This site is an open area with agave plant cultivation and extensive grazing areas; canopy cover is 1% with an arboreal density of eight individual trees/ha; 50% of the land is used for cultivation of agave plants (*Agave angustifolia*), 20% for induced pasture, 10% for living fences (*Prosopis*, *Yucca*, *Celtis*, *Acacia*, *Opuntia*, and *Schinus*), and 20% of the surface has no vegetation (exposed floor; Torres-Barragán 2015).

Data Collection

Twelve sampling events were conducted at each site (UA and DA) from January 2014 to January 2015. Each sampling event was carried out over a single three-day period in each month at each of the two sites (for a total of six sampling days per month), with a sampling effort of three people from 0900–1800 h.

The method of mark-recapture of Lemos-Espinal and Ballinger (1995) and Ramírez-Bautista (1995) was used in this study. This method consisted of ectomization of phalanges (e.g., toe-clipping), a permanent marking technique that makes it possible to recognize every previously marked individual during each subsequent sampling event. Toe-clipping is commonly used to follow cohorts of lizard populations (Dunham 1978; Tinkle 1961, 1969). More recently, Guimaraes et al. (2014) and Olivera-Tlahuel et al. (2017) expressed some concern when using this method due to observed effects on the

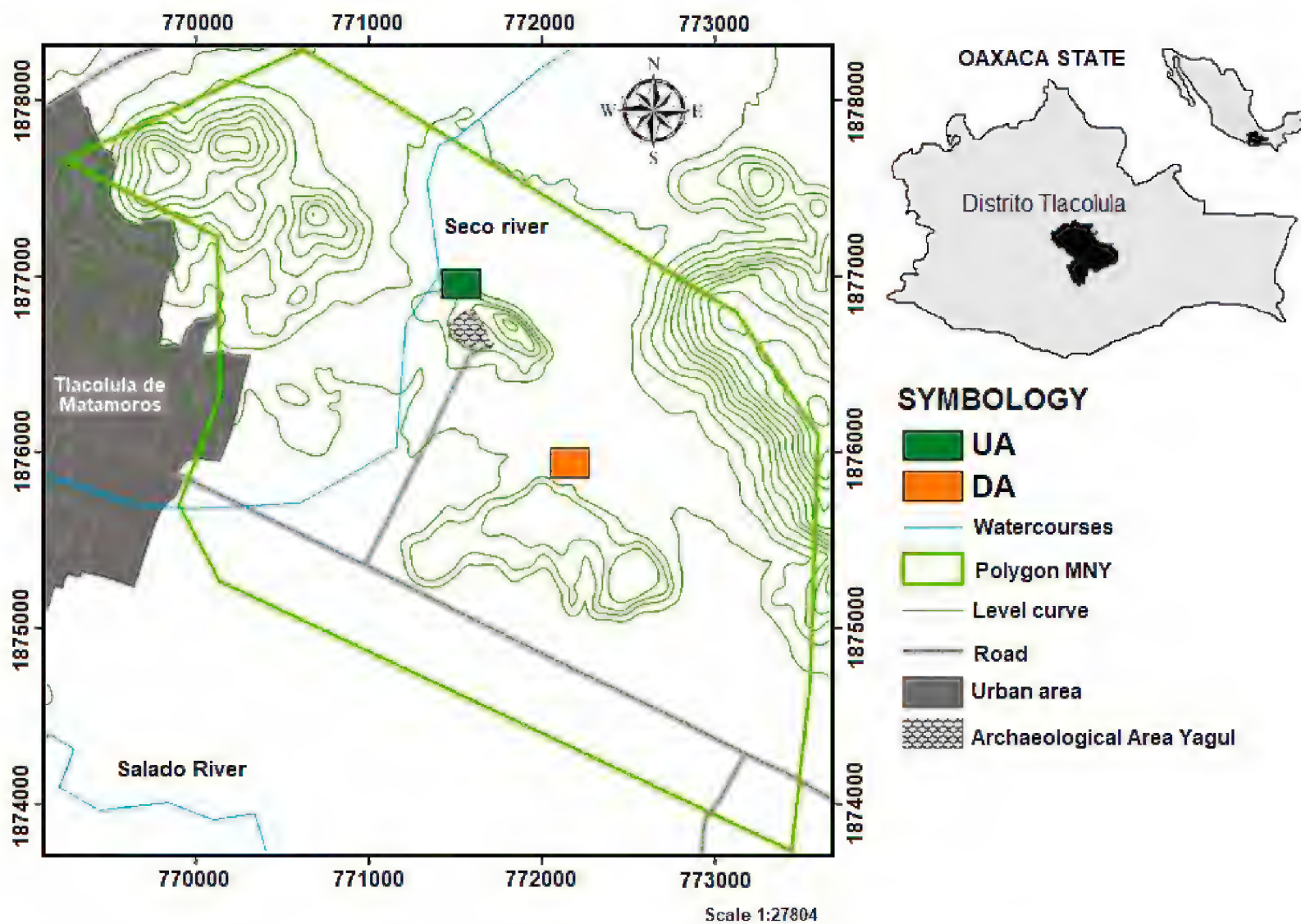


Fig. 1. Map of the study area. The green polygon depicts Yagul Natural Protected Area, including the two sampling sites (UA = undisturbed area; DA = disturbed area, land use change).

behavior and health of some lizard species, and therefore, on survival. Although toe-clipping could affect survival, lizards at both sites were toe-clipped similarly, so any negative bias in survival estimates should apply equally to both sites. The SVL of each lizard was measured with a digital caliper (to the nearest 0.01 mm), and body mass with a balance (± 0.01 g).

Relative Density and Population Structure

Based on the number of captured and recaptured individuals from both populations during the study, the relative density of each population was determined using the equation, $N = M/R$, where N = number of unknown individuals in the population; M = the number of marked individuals; and R = the number of recaptured individuals/surface area. To determine the population structure for each site, size classes (SVL) were determined based on those used by Leyte-Manrique et al. (2017) with *Sceloporus grammicus*. These authors related the SVL of each age category based on anatomical traits, yielding classification categories of: offspring (SVL ≤ 48 mm), juveniles (49–69 mm), and adults (females and males ≥ 70 mm). Females were considered to be adults if they contained eggs in the oviduct, which were identified by palpation of the ventral region (Galán 1997). Whereas males were considered to be adults when they showed the bulky tail base indicative of sperm production (Lozano et al. 2014). Relative densities of lizards were compared

between locations and seasons by means of a Student's t -test (Zar 2014).

Growth Rate

Growth rates were assessed for males and females from each population by considering only those lizards with recapture intervals greater than 30 and less than 100 days. Therefore, growth rate was estimated with the formula: $GR = (SVL_2 - SVL_1)/days$, where growth rate (GR) is the difference in recorded SVL between the last recapture (SVL₂) and first capture (SVL₁) divided by the number of days that had elapsed (Dunham 1978; Zamora-Abrego et al. 2012). Then, nonlinear regression models of Von Bertalanffy, logistic by body size (SVL), and logistic by body mass were used (Dunham 1978); and growth rates for both sexes and populations were compared. The first model (Von Bertalanffy) describes a pattern in which smaller individuals (in SVL) show faster growth rates than larger ones (Dunham 1978; Zamora-Abrego et al. 2012). In contrast, the logistic models predict that individuals smaller in SVL will grow moderately faster to reach intermediate sizes, and after reaching their maximum growth rate, that rate will decrease in a non-linear direction as size increases (Dunham 1978; Schoener and Schoener 1978; Zamora-Abrego et al. 2012). The difference between the two models is that the maximum growth rate attained under a logistic by length (SVL) model is observed at early ages, while maximum growth rate under a logistic by body mass model will

be observed at later ages (Dunham 1978). Detailed descriptions of each model can be reviewed in Dunham (1978) and Schoener and Schoener (1978). Selection of the best model was based on the best fit to the observed growth rates for both sexes, chosen by the lowest value of the residual mean square (RMS) and highest values of coefficients of determination or correlation (R^2 ; Dunham 1978; Schoener and Schoener 1978).

Once selected, the models were developed with confidence intervals following Schoener and Schoener (1978) for the growth parameter (r), and the asymptotic (A_1) was calculated by the formula:

$$\theta_j - \sqrt{kF_{1-\alpha}(k, N-k)S_j^2} \leq \beta_j \leq \theta_j + \sqrt{kF_{1-\alpha}(k, N-k)S_j^2}$$

where β_j is the adjusted parameter j , θ_j is the parameter estimated β_j , S_j is the asymptotic standard deviation of β_j , $F_{1-\alpha}(k, N-k)$ is the value $F_{1-\alpha}$ of a tail with k and $N - k$ degrees of freedom, N is sample size, and k is the number of adjusted parameters. These confidence intervals provide maximum reliability for each parameter (r and A_1) and are considered significantly different between sexes if they do not overlap (Schoener and Schoener 1978). On the other hand, the residuals of the growth rate (removal of effect size) were used to determine by two-way ANOVA if there were differences in the patterns of growth rates between factors (sexes and populations). The residuals are the result of the relationship between the SVL and the growth rate under the model with the best fit (Schoener and Schoener 1978). Finally, based on the values of the growth parameter (r) and asymptotic (A_1) obtained from the best-fit model, together with the average values of SVL of offsprings at hatching ($L_0 = 42$ mm in SVL), the ages in days were determined for both males and females at which they reach sexual maturity (Dunham 1978; Schoener and Schoener 1978; Zamora-Abrego et al. 2012). The growth models for both sexes and populations were developed with Statistica program, version 7.0.

Estimates of the Survival Models

Captures and recaptures of marked individuals allowed estimates of demographic parameters, such as survival (ϕ) and recapture (p); and both parameters were estimated from different models that represent distinct biological hypotheses of survival (Lebreton et al. 1992). Both ϕ and p can be constant (c) over time or vary as a function of time (t) and between sex, and for their assessment a general model was considered which allowed the determination of whether survival rates and recaptures were different between sexes and populations. This model is: ϕ (groups [males and females in two populations = four groups]*time) p (groups*time), and it calculates the probability that survival and rate of recapture are different between groups over different periods of time.

For developing the different models based on encounter histories of each individual (e.g., 100101), zero represents sampling when a lizard was not seen in the area, while 1 represents those sampling events when lizards were marked and recaptured (Lebreton et al. 1992). Encounter histories were analyzed and modeled with software Mark 6.0 (White and Burnham 1999) using the subprogram “only recaptures” with the goal of obtaining estimates of survival and recapture rates grounded in the techniques of maximum likelihood under the model developed by Cormack-Jolly-Seber (Lebreton et al. 1992). The model that showed the best fit to the capture-recapture data was the one with the lower Akaike information criterion (AIC) value; however, when there was a difference of 2 between AIC values of the two models, both models were assumed to have approximately the same fit to the data (Burnham and Anderson 2002). Survival and recapture results are represented with confidence intervals of 95%.

Results

Relative Density and Population Structure

In the surveys, 271 individuals were marked across both sites (UA = 149 and DA = 122); of these, 113 were recaptured (73 in UA and 40 in DA; Table 1). In some cases, several individuals were captured as juveniles and then recaptured as adults; but most of the recaptures were adult males and females (Table 1). The relative density between seasons was different ($t_{1,11} = -2.023$, $P = 0.05$; wet: 6.95 ± 0.41 [4.92–10.07]; dry: 9.70 ± 1.29 [2.68–17.21]), but not between populations ($t_{1,11} = -0.116$, $P = 0.98$; UA: 8.33 ± 0.97 [5.68–16.11]; DA: 8.33 ± 1.11 [3.28–17.21]). The relative density for UA (both sexes and all age classes) was 149 individuals/ha, whereas for DA it was 122 individuals/ha. In UA, offspring emerged from July to December, but the peak hatching period was in September; juveniles were recorded from October to April, but the highest population of this age class was in December; adults were present throughout the year, but the highest numbers of captures were in April and May (Table 1). Offspring from DA were found from August to November, with peak density in August; juveniles appeared from October to March, with density peaking in December; and adults were seen from September to July, with the greatest densities from April to May (Table 1).

Growth Rate

The length logistic model showed the best fit to the growth rate data for males and females from UA; in contrast, the Von Bertalanffy model showed the best fit to the growth rate data for both males and females of DA (Fig. 2 and Table 2). The logistic model by length showed that growth rates for males ($r \pm EE$: 0.007 ± 0.0005) and females ($r \pm EE$: 0.008 ± 0.0008) from UA were similar, whereas the asymptotic growth curve of females ($A_1 \pm$

Table 1. Numbers of *Sceloporus spinosus* individuals in each age class during each study month at Yagul Natural Protected Area. UA = Undisturbed area, DA = Disturbed area. * Indicates the rainy months. A = adult, J = juvenile.

UA	Offspring		Juveniles		Adults		Recaptures
Samples	Males	Females	Males	Females	Males	Females	
January	0	0	1	2	1	0	0
February	0	0	3	4	2	1	1♀A
March	0	0	2	4	7	2	3♂A, 1♀, 2♀J
April	0	0	3	3	9	9	4♂A, 5♀, 2♂J
May	0	0	0	0	7	10	4♂A, 5♀A
June*	0	0	0	0	2	6	1♂A, 5♀A
July*	0	1	0	0	7	4	5♂A, 2♀A
August*	3	1	0	0	2	3	2♀, 1♂J
September*	3	2	0	0	5	1	3♂A, 1♀A, 2♂J
October	3	1	0	1	4	3	3♂A, 2♀A, 2♂J, 1♀J
November	4	0	3	2	6	0	5♂A, 2♂J, 1♀J
December	1	0	7	2	2	0	5♂A, 3♀A
Density (#/area)	0.0019		0.0037		0.0093		
Total	14	5	19	18	54	39	73
DA	Offspring		Juveniles		Adults		Recaptures
Samples	Males	Females	Males	Females	Males	Females	
January	0	1	2	2	2	2	0
February	0	0	1	0	2	1	0
March	0	0	2	2	5	3	1♂A
April	0	0	0	0	10	6	6♂A, 3♀A
May	0	0	0	0	11	10	4♂A, 5♀A
June*	0	0	0	0	1	5	2♀A, 1♂A
July*	0	0	0	0	4	5	5♂A, 2♀A
August*	3	4	0	0	0	0	0
September*	1	2	0	0	1	3	0
October	1	0	2	4	0	2	1♀J, 2♀A
November	1	0	4	2	0	2	1♀A, 3♂J
December	0	0	5	6	1	1	1♂A, 1♀, 2♀J
Density (#/area)	0.0013		0.0032		0.0077		
Total	6	7	16	16	37	40	40

EE: 105.359 ± 3.225 mm) was slightly higher than that of males ($A_1 \pm$ EE: 101.706 ± 1.587 mm; Table 2). On the other hand, for males and females from DA, the Von Bertalanffy model showed that male ($r \pm$ EE: 0.005 ± 0.0008) and female ($r \pm$ EE: 0.005 ± 0.0011) growth rates were similar (Table 2); however, the females reached an asymptotic size (maximum size) that was slightly larger ($A_1 \pm$ EE: 108.058 ± 4.139 mm) than the males ($A_1 \pm$ EE: 103.253 ± 3.723 mm; Table 2). Average values of the residuals of growth rates for males and females from UA, obtained with both the logistic by length model and a two-way ANOVA, did not show significant differences (males: -0.001 ± 0.009 ; females: 0.003 ± 0.019) between dry ($F_{1,29} = 0.047$, $P = 0.8300$) and wet seasons ($0.001 \pm$

0.010 , -0.004 ± 0.011 , respectively), between sexes ($F_{1,29} = 0.003$, $P = 0.9577$), or interactions between factors (season*sex; $F_{1,29} = 0.116$, $P = 0.7358$). A similar pattern occurred for DA, where no differences were found in males (-0.003 ± 0.013) and females (-0.007 ± 0.015) between dry and wet seasons ($F_{1,24} = 0.975$, $P = 0.3333$; males = 0.021 ± 0.009 and females = 0.015 ± 0.033), between sexes ($F_{1,24} = 0.044$, $P = 0.8358$), or interactions between factors (season*sex; $F_{1,24} = 0.004$, $P = 0.9472$).

On the other hand, there were no differences in the overall growth rates of males from the two populations ($F_{1,31} = 0.234$, $P = 0.6317$), in neither dry (UA: -0.001 ± 0.009 ; DA: -0.003 ± 0.013) nor wet (UA: 0.001 ± 0.010 ; DA: 0.021 ± 0.009) seasons ($F_{1,31} = 0.535$, $P = 0.4699$);

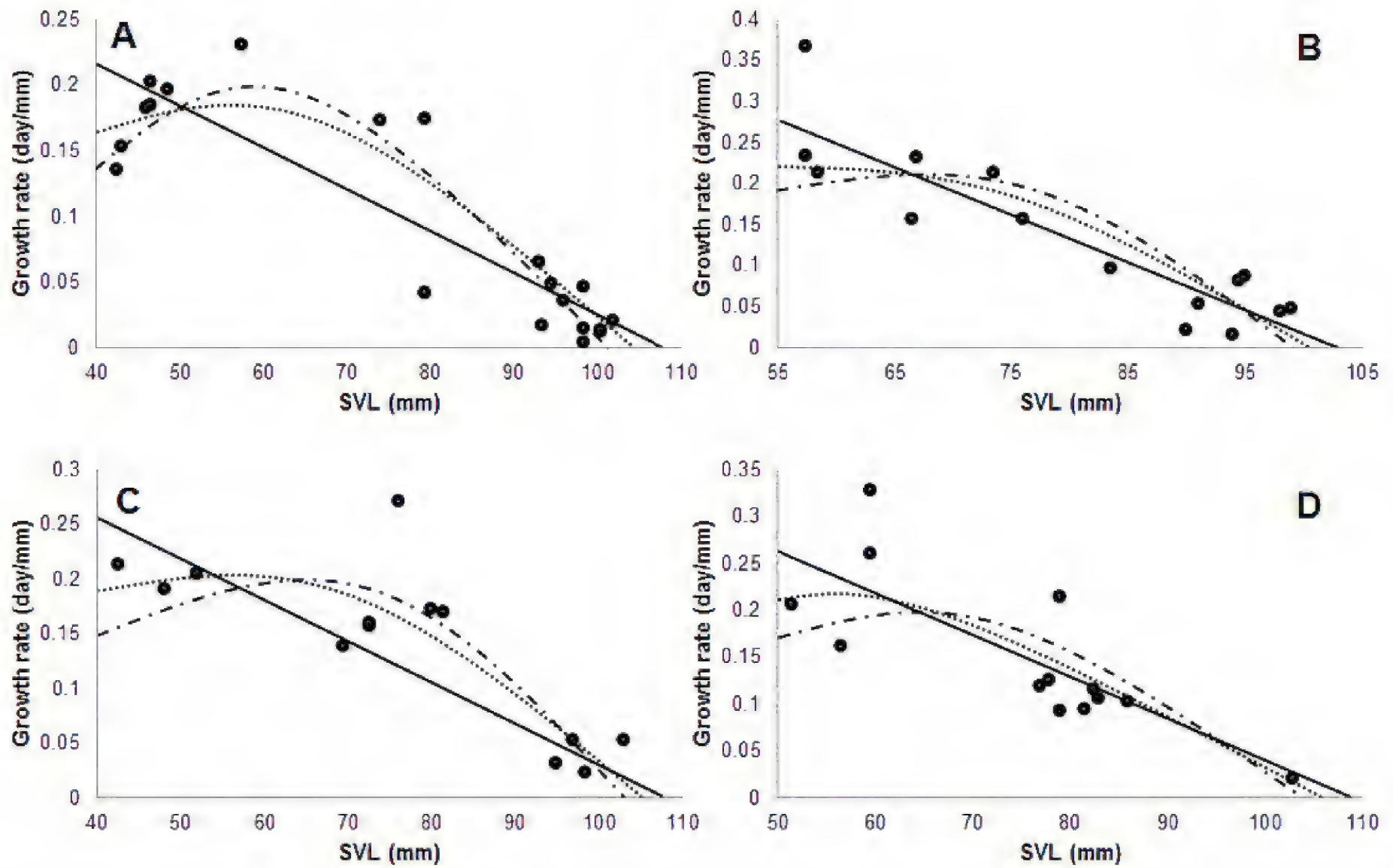


Fig. 2. Growth rate of *Sceloporus spinosus*. (A) Undisturbed area (UA) males, (B) Disturbed area (DA) males, (C) UA females, and (D) DA females. Black circles represent data points for individual lizards. Modeled relationships between growth and body sizes of males and females: solid lines = Von Bertalanffy, dashed lines = logistic by length, and dotted lines = logistic by mass.

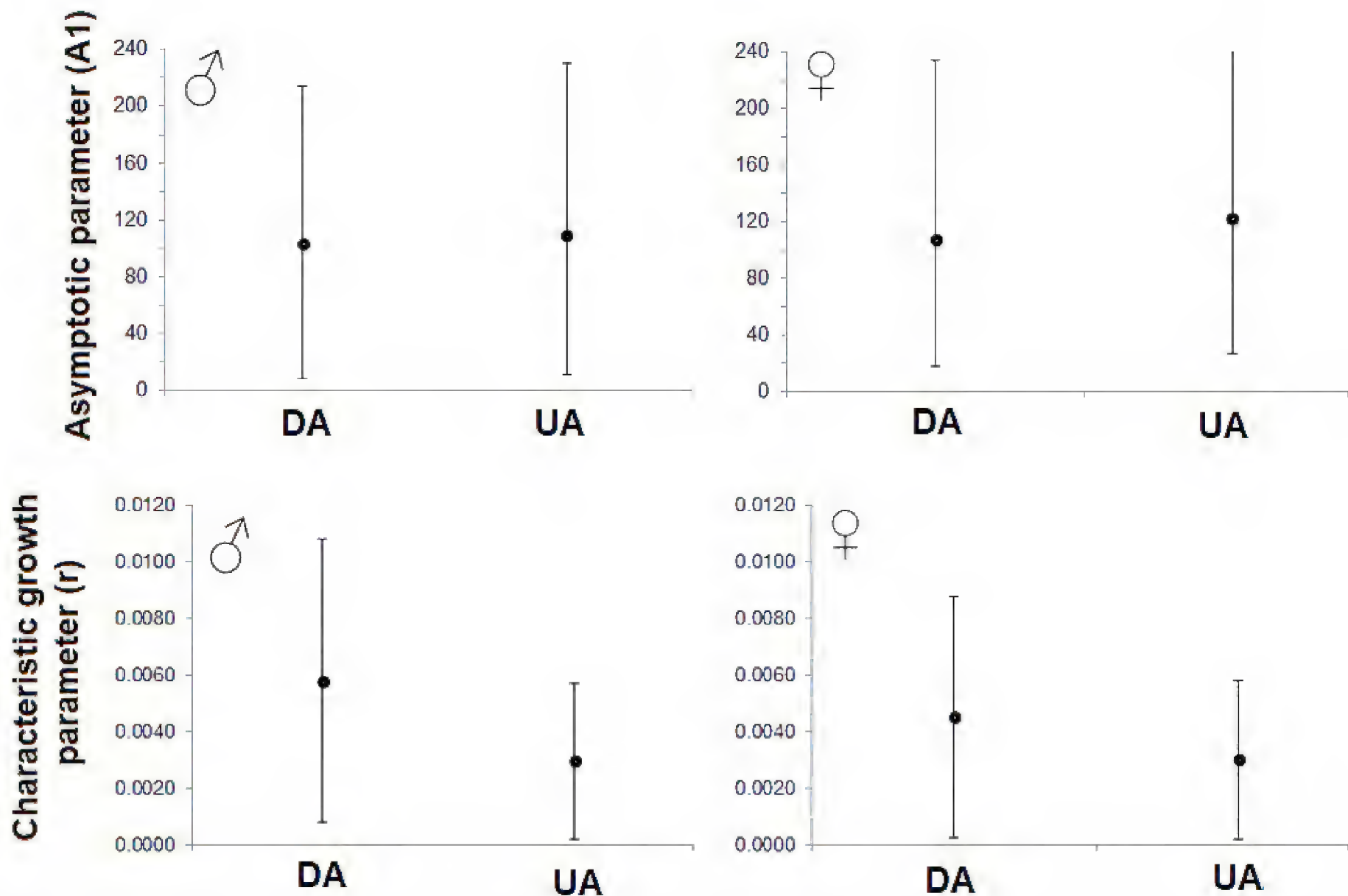


Fig. 3. Means and 95% confidence intervals of the Asymptotic growth (A_1) and Characteristic growth (r) parameters obtained by the Von Bertalanffy and logistic by length models for males and females of *Sceloporus spinosus* in both Disturbed area (DA) and Undisturbed area (UA) populations.

therefore, the interaction term (locality*season) was not significant ($F_{1,31} = 0.401$, $P = 0.5312$). The same pattern was found in females, as there were no differences between localities ($F_{1,22} = 0.057$, $P = 0.8130$), or seasons ($F_{1,22} = 0.124$, $P = 0.7284$); and, therefore, the interaction term (locality*season) was also not significant ($F_{1,22} = 0.587$, $P = 0.4519$).

Growth parameters (r and A_1) were similar for males and females in UA and DA populations (Fig. 3); confirming that there is no difference between the sexes. In UA, the growth rate showed that males reached sexual maturity at SVL 85 mm at age 210 d (7 months), whereas females attained sexual maturity at SVL 89 mm at age 280 d (9 months). In DA, males reached sexual maturity at SVL 81 mm at age 210 d, and females at SVL 85 mm at age 280 d.

Survival Model Estimation

To analyze survival rate (ϕ) and recapture (p) of *S. spinosus* in UA and DA populations, a set of models was developed (Table 3). The single model that described survival rate as varying between groups (sexes) and where the recapture rate was constant [$\Phi(\text{sex})p(c)$] was chosen as the best fit for both populations (Table 3A). Based on this model, the survival rate for males from

UA (0.82) was higher than that of females (0.70), while the recapture rate was similar for both sexes (0.40; Table 4A). In addition, the survival rate for males from DA (0.75) was higher than that of females (0.65), and the probability of recapture was higher for males (0.40) than for females (0.35; Table 4A). These values are lower than those found for UA, which suggests a higher probability of survival and recapture in UA than DA. On the other hand, survival and recapture rates by season (wet and dry) in UA and DA populations showed that the model with the best fit was $\Phi(c)p(\text{season})$, indicating that survival rate is constant, and the probability of recapture varies between seasons (Table 3B). According to this model, the survival rates in both populations were higher in the dry (UA: 0.76, DA: 0.92) than the wet (UA: 0.54, DA: 0.49; Table 4B) season.

Discussion

More lizards were marked at the UA site than the DA site during this study. However, at both UA and DA the greatest numbers of adult recaptures were in April and May, due to the peak in reproductive activity during these months (Valdéz-González and Ramírez-Bautista 2002). According to the recapture data, lizards born in August-September reached the minimum SVL at sexual

Table 2. Growth parameters for *Sceloporus spinosus* males and females from UA and DA populations obtained from each growth model. RMS = residual mean square, R^2 = coefficient of determination, A_1 = asymptotic of growth, r = parameter of growth, \pm = standard error.

UA	Model	RMS	R^2	A_1	r
Males ($n = 20$)					
	Von Bertalanffy	0.029	0.730	109.480 \pm 5.223	0.003 \pm 0.0003
	Logistic by length	0.019	0.849	101.706 \pm 1.587	0.007 \pm 0.0005
	Logistic by weight	0.025	0.797	100.081 \pm 1.114	0.012 \pm 0.0009
Females ($n = 13$)					
	Von Bertalanffy	0.029	0.595	122.243 \pm 12.423	0.003 \pm 0.0007
	Logistic by length	0.019	0.736	105.359 \pm 3.225	0.008 \pm 0.0008
	Logistic by weight	0.023	0.687	102.482 \pm 2.221	0.012 \pm 0.0011
DA	Model	RMS	R^2	A_1	r
Males ($n = 15$)					
	Von Bertalanffy	0.027	0.809	103.253 \pm 3.723	0.005 \pm 0.0008
	Logistic by length	0.035	0.756	99.762 \pm 2.410	0.0099 \pm 0.0010
	Logistic by weight	0.048	0.664	98.523 \pm 1.995	0.0141 \pm 0.0016
Females ($n = 13$)					
	Von Bertalanffy	0.030	0.625	108.058 \pm 4.139	0.005 \pm 0.0011
	Logistic by length	0.032	0.601	100.178 \pm 3.225	0.008 \pm 0.0012
	Logistic by weight	0.429	0.046	99.340 \pm 3.7378	0.012 \pm 0.0017

Table 3. Models describing survival rate (ϕ) and recapture (p) of *Sceloporus spinosus* males and females in UA and DA with the Jolly-Saber model using the Mark program. The models are fitted with the Mark program considering that Φ y p (probability of survival and recapture) can be either constant (c) or varying between sex (s), season (dry and wet), and population. AIC = Measurement of the level of adjustment and parsimony of each model, Δ_i = difference of AIC, W_i = weight of AIC, K = number of parameters.

A. Models for estimation of sex and populations.

Model	AIC	Δ_i	W_i	K
Φ (sex) p (c)	231.98	0	0.69	12
Φ (c) p (c)	234.09	2.11	0.24	13
Φ (population) p (c)	238.22	6.25	0.03	12
Φ (population) p (sex)	240.54	8.57	0.01	13
Φ (sex) p (c)	241.68	9.71	0.01	3
Φ (c) p (sex)	242.11	10.13	0	3
Φ (population) p (population)	243.39	11.42	0	21
Φ (sex) p (sex)	243.84	11.86	0	4

B. Models for estimation of season (dry and wet) and populations.

Model	AIC	Δ_i	W_i	K
Φ (c) p (season)	227.02	0	0.88	3
Φ (season) p (c)	231.98	4.96	0.07	12
Φ (season) p (population)	237.17	10.16	0.01	3
Φ (c) p (c)	240.11	13.1	0	2
Φ (t) p (t)	243.39	16.38	0	21
Φ (population) p (season)	247.87	20.86	0	2

maturity (> 80 mm) in April-May of the following year, a similar pattern seen in another population of the same species (Valdéz-González and Ramírez-Bautista 2002). Recruitment of offspring, together with adult males and females, and a few subadults, results in population growth with respect to these age structures. These events are synchronized with an increase in ambient temperatures (from 20.9 °C in April to 21.2 °C in May) and precipitation (from 113.3 mm in June to 114.4 mm in May) in the region, which also coincide with high production of food in the environment (Dunham 1982; Ramírez-Bautista and Vitt 1997).

In general, these results revealed that lizard density was significantly similar between populations, but not between seasons (higher in the wet season than in the dry season). The higher density of lizards found in the wet season could be explained by a high supply of the food consumed by this species. However, this assumption brings up additional questions regarding the feeding habits of other species living in sympatry with *S. spinosus* in disturbed and undisturbed environments. Therefore, it is necessary to investigate whether those sympatric species have the same possibilities of acquiring available resources (food and microhabitat), or if they

display different activity schedules that allow them to obtain resources more efficiently. Such studies would certainly expand our knowledge on the natural history of this species, and consequently enable the development of more effective conservation strategies.

The growth rate models used here showed that males and females in both populations grow at the same rate and reach maximum SVL at similar sizes. These results were found by the logistic model by length (UA) and Von Bertalanffy (DA), models that are known to fit most growth analyses for at least some lizard species of the family Phrynosomatidae (Lemos-Espinal and Ballinger 1995; Zuñiga-Vega et al. 2008; Pérez-Mendoza et al. 2014; Ramírez-Bautista et al. 2016). The pattern of low growth rate variation in both populations observed in this study could suggest that populations of this species are able to inhabit areas with certain degrees of disturbance, as has been shown in other species of lizards analyzed by D’Cruze and Kumar (2011) in both disturbed and undisturbed environments.

On the other hand, a homologous pattern in growth rates for males and females in both UA and DA populations may be due to the similarities in SVL at birth and the SVL at sexual maturity. For the former (SVL at birth), growth rates are likely to be regulated by predation intensity, acting mainly on offspring and juveniles of both populations (Schoener 1979; Andrews 1982). This interpretation could be different if both demographic parameters (survivorship and recaptures) evaluated for each site had changed based on an increased number of recaptures. This pattern has also been observed in populations of *S. grammicus* from Central Mexico (Pérez-Mendoza et al. 2013, 2014).

The life history characteristics studied here for this species could have significant plasticity among its populations, and therefore, small differences in temperature, precipitation, and food between UA and DA would not have apparent effects (Valdez-González and Ramírez-Bautista 2002; Valencia-Limón et al. 2014). A similar pattern in growth rates also occurs between sexes and age classes in other lizard genera (e.g., *Xenosaurus* spp.; Molina-Zuluaga et al. 2013).

The low variation in SVL at sexual maturity observed in the growth curve within and between populations is partially explained by the absence of sexual dimorphism with respect to SVL (Valdéz-González and Ramírez-Bautista 2002; Ramírez-Bautista et al. 2013). Walkup et al. (2017) pointed out that *Uta stansburiana*, *Aspidoscelis marmorata*, *A. sexlineata*, and *Sceloporus consobrinus* present generalist habits in microhabitat choice, being able to inhabit sites with different degrees of disturbance. Consequently, these species tend to present reduced variation in some of their demographic characteristics, as a measure of phenotypic plasticity towards different degrees of environmental disturbance.

In this study, lizards from UA were numerically more abundant and showed a slightly higher survival rate

Table 4. Probability of total survival (ϕ) and recapture (p) for both sexes and season for UA and DA populations. SE = standard error.**A. Survival values and recapture between sexes**

Undisturbed area (UA)			Disturbed area (DA)		
Parameters	Estimation	SE	Parameters	Estimation	SE
Φ (males)	0.822	0.042	Φ (males)	0.75	0.019
p	0.402	0.051	p	0.40	0.024
Φ (females)	0.706	0.056	Φ (females)	0.65	0.061

B. Survival values and recapture between seasons

Undisturbed area (UA)			Disturbed area (DA)		
Parameters	Estimation	SE	Parameters	Estimation	SE
Φ (dry)	0.765	0.036	Φ (dry)	0.927	0.078
Φ (wet)	0.538	0.074	Φ (wet)	0.489	0.072

than those from DA. This suggests that relative density may be a measure of population variation that predicts the survival value for both sites. However, in some cases lower survival probability has been observed in populations with high density than in populations with low density (Stearns 1992; Zúñiga-Vega et al. 2008).

Survival rates and probabilities of recapture obtained here for males and females were higher compared to those reported for *Anolis nebulosus* (Hernández-Salinas 2014), *Xenosaurus grandis* (Zúñiga-Vega et al. 2007), and *Sceloporus grammicus* (Pérez-Mendoza et al. 2014). The models used in these studies considered sex, season (dry and wet), and populations as variables that express the greatest sources of variation, similar to the survival rate assessed in other species of the genus *Sceloporus* (Zúñiga-Vega et al. 2008; Pérez-Mendoza et al. 2014). The results for survival obtained here were similar to those of other studies (Zúñiga-Vega et al. 2008; Molina-Zuluaga et al. 2013; Hernández-Salinas 2014) where survival and recapture rates were found to be higher in males and females in one population during the dry season. One possible explanation is that the reproductive activity of this species begins during the rainy season, causing males to search for mates for reproduction, participating in male-male agonistic competition, and consequently becoming more susceptible to predation (Sinervo et al. 1991). In contrast, for females, survival rates have been observed to decrease dramatically at the end of the gestation stage and parturition (end of the rainy season), possibly because pregnant females become heavier and slower, therefore increasing the risk of predation during the wet season (Clobert et al. 1998, 2000; Stearns 1992; Zúñiga-Vega et al. 2008). This pattern also has been observed in other lizard species, such as *Anolis nebulosus* from tropical dry forest (Ramírez-Bautista and Vitt 1997).

Conclusions

This study found little variation regarding growth rate, survival, and body size at sexual maturity between

populations of *Sceloporus spinosus*. This supports the assumption that the toe-clipping method did not impair the performance of individuals in both populations, allowing the results of this study to be comparable with future works. For the above, and contrary to our expectations, this study showed that males and females in both UA and DA showed similar growth rate patterns, with both sexes reaching sexual maturity at similar SVL in both populations. The results obtained here may not be regarded as the variation typically observed in these life history attributes (growth, survival, and SVL at maturity), since the minimal variation observed in these characters may indicate that they are genetically fixed components, as has been determined in some species of *Xenosaurus* (Zúñiga-Vega et al. 2005, 2007; Zúñiga-Vega 2011) and *A. nebulosus* (Ramírez-Bautista and Vitt 1997). The results of this study should be taken with caution, since further studies are needed to determine the effects of temperature, precipitation, competition, and food on the life-history characteristics of the species living in both environments. Additional studies will support more solid conclusions regarding the growth, survival rate, and size at sexual maturity across the entire distribution range. In order to improve these results, we also suggest the development of hypotheses aimed at determining the relative abundance of predators. Furthermore, it is necessary to develop elasticity and sensitivity analyses with larger sets of capture-recapture data to better comprehend the effects of environmental pressures on the life history characteristics of a species that is found in both intact environments and environments with varying degrees of disturbance.

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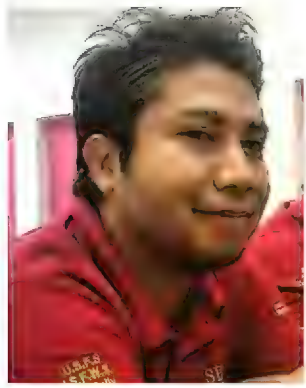
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